THE SPERMATHECAL PORES OF SPIDERS WITH SPECIAL REFERENCE TO DICTYNOIDS AND AMAUROBIOIDS (ARANEAE, ARANEOMORPHAE, ARANEOCLADA)

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Abstract   *Proc. ent. Soc. Ont.* 123:1-21

Two types of spermathecal pore structures occur in the vulvae of spiders. One or more simple "primary" pores of uncertain function are well known but not often discussed. Likely they are plesiomorphically present in all spiders. Complex "dictynoid" pores (probably an apomorphy of Dictynoidea) of unknown function are here described for the first time and their distribution in spiders is examined. The placement of primary and dictynoid pores is used to identify homologous regions among the vulvae of the taxa examined.

Introduction

The copulatory organs are the most important indicators for identifying spider species and can provide valuable characters for phylogeny reconstruction. Coddington (1990b) and Sierwald (1989, 1990) have lamented the lack of information about homologies among male palpal sclerites and female vulval components above the family level. Simple pores penetrating the spermathecae of spiders (Figs. 2, 5, 12, 18) are of very widespread occurrence and may be plesiomorphically present in all female spiders (Forster *et al.* 1987; Sierwald 1989). As such, and assuming they are homologous, these pores can serve as important markers of homologous regions in the spermathecae of diverse taxa.

In spite of their acknowledged widespread occurrence spermathecal pores have been virtually ignored as taxonomic characters. Among taxonomic and systematic works only those dealing with liphistiomorphs (e.g. Platnick and Sedgwick 1984), mygalomorphs (e.g. Coyle 1981; Goloboff and Platnick 1987; Griswold 1987), and the most primitive araneomorphs (palaeocribellates and austrochiloids: e.g. Forster *et al.* 1987) routinely discuss or at least illustrate spermathecal pores. Perhaps this is because the pores are prominent features of the relatively simple saccate spermathecae in these spiders. The vast majority of spider taxonomic and systematic literature deals with the "higher" araneomorphs (Araneoclada—haplogynes and entelegynes) in which the spermathecae are generally much more complex. In these works spermathecal pores are rarely mentioned or illustrated (even the most recent general spider biology text [Foelix 1982] gives them only meagre coverage). Only Sierwald (1989), in determining homologies amongst pisaurid spermathecae, appears to have recently addressed spermathecal pores.

Little is known of their function. Passage of secretions into the spermatheca is undeniable: many authors have demonstrated that glands envelope the pores and drain through them into the spermatheca (e.g. Petrunkevitch 1925; Opell 1979, 1983; Kovoor 1981; Coyle *et al.* 1983; Lopez and Juberthie-Jupeau 1983; Forster *et al.* 1987). Several hypotheses of function, not necessarily

mutually exclusive, have been proposed but remain unproven. These (briefly reviewed in Lopez 1987) include pheromone production (Kovoor 1981), sperm nutrition (Forster 1980; Coyle *et al.* 1983) and/or activation (Lopez and Juberthie-Jupeau 1983; references in Opell 1983), and mechanical displacement of sperm from the spermathecae into the fertilization ducts during fertilization (Forster *et al.* 1987; Lopez 1987).

Some spiders have two types of spermathecal pores: simple ones as discussed above as well as more complex ones (described below) usually located on the spermathecae near the fertilization ducts (Figs. 1, 4, 7, 12). Prior to this study these complex pores were unknown although Roth (1952: 213, 215, 218), in a study of *Cybaeus* L. Koch, briefly mentioned nonconformities on the surface of the spermathecae which are undoubtedly the complex pores. During the preparation of a revision of the Nearctic Cybaeidae (Bennett 1991) I studied the complex pores in depth. At first it seemed these pores could be an apomorphy defining Cybaeidae but it soon became apparent that they are more generally distributed. They may be synapomorphic for most, if not all, Dictynoidea *sensu* Forster (1970), a grouping encompassing the entelegyne families Dictynidae, Megadictynidae, Hahniidae, Desidae, Cybaeidae, Argyronetidae, and Anyphaenidae (including Amaurobioididae) (see Coddington [1989] for a discussion of the monophyly of Dictynoidea.) For this reason the simple spermathecal pores are here referred to as "primary" pores and the more complex ones as "dictynoid" pores.

Where spider vulval ontogeny has been examined in detail, the primary pores are evident at a very early stage (Bhatnagar and Rempel 1962; Sierwald 1989; Bennett 1991). Dictynoid pores, however, apparently develop only in the final stages (Bennett 1991).

Methods

The following entelegyne taxa were examined for the presence of dictynoid pores particularly, but also for primary pores. Vulvae with dictynoid pores are described in greater detail than those without.

Except for *Callioplus*, *Dictyna*, *Neoantistea*, *Phrurotimpus*, and *Hogna* these taxa are/were members of the polyphyletic Agelenidae *sensu lato* and were selected because of an underlying interest in the true relationships of the traditional agelenids, especially the cybaeids. Lehtinen's (1967) radical redefinition of the Agelenidae resulted in most of the familial placement recorded below. Modifications from Lehtinen's classification (e.g., coelotines in the Amaurobiidae) follow the catalogue of Platnick (1989). Both Brignoli (1983) and Platnick (1989) accepted the majority of Lehtinen's changes but expressed concerns (Lehtinen's taxonomic novelties are not based on definitive apomorphies—but see Griswold's [1990:13, 20] discussion of Lehtinen's concept of Agelenidae).

Amaurobioidea:
Agelenidae: *Agelenopsis potteri* (Blackwall), *Tegenaria domestica* (Clerck).
Amaurobiidae: *Callioplus macarius* Chamberlin, "*Coelotes*" sp., *Coras juvenilis* (Keyserling),
                       Rubrius antarcticus (Karsch), *Wadotes calcaratus* (Keyserling).
Lycosidae: *Hogna helluo* (Walckenaer).

Dictynoidea:
Argyronetidae: *Argyroneta aquatica* (Clerck).

Dictynidae:	*Blabomma californica* (Simon), *Cicurina bryantae* Exline, *C. intermedia* Chamberlin and Ivie, *Cicurina* sp., *Dictyna coloradensis* Chamberlin, *Yorima angelica* Roth.
Cybaeidae:	*Cybaeus* spp., *Cybaeota shastae* Chamberlin and Ivie, *Cybaeozyga heterops* Chamberlin and Ivie
Hahniidae:	*Calymmaria montavencis* (Bishop and Crosby), *Calymmaria* sp., *Cryphoeca exlineae* Roth, *Dirksia cinctipes* (Banks), *Ethobuella tuonops* Chamberlin and Ivie, *Neoantistea* sp., *Neocryphoeca beattyi* Roth, *N. gertschi* Roth.

Uncertain placement:

Liocranidae:	*Phrurotimpus borealis* (Emerton).

In this paper Sierwald's (1989) terms for the components of the female spider's copulatory organs are followed in an effort to standardize names of presumably homologous parts in different taxa. Thus epigynum refers to the external components including the atrium or atria which is/are one or two cavities leading into the vulva. The vulva is comprised of the paired internal components: the copulatory ducts (joining the atrium/atria to the spermathecae), the spermathecae (in which sperm are stored and the pore structures are located), and the fertilization ducts (through which sperm pass from the spermathecae to the uterus externus during fertilization). Each spermatheca has a head (containing the primary pores), stalk (with usually one dictynoid pore if such pores are present), and base. In many taxa these divisions are not distinct and can only be determined by the presence of pores. See Bennett (1991) for a discussion of the homology of the female copulatory organ components in various spider taxa.

Specimens used in this study are in the author's collection unless otherwise stated. Vulvae were excised from spiders preserved in 75% ethanol, cleared in clove oil, and examined with a Leitz Laborlux compound microscope. Some were cleared with a commercial contact lens cleaner solution (Sierwald 1991), dehydrated in absolute ethanol, mounted on standard SEM stubs, and sputter coated with gold palladium prior to examination in an S-570 Hitachi scanning electron microscope.

Abbreviations used in figures are explained in the legends for Figures 1-14.

Results

Pore Structure and Placement

Primary pores are simple canals which convey gland ducts through the walls of the spermathecal heads. Histological sectioning and staining techniques are normally needed to demonstrate the glandular tissue associated with the primary pores but often in specimens cleared with clove oil or contact lens cleaner the gland ducts or remnants of them (Figs. 2, 32) appear as small, lightly sclerotized threads emanating from the pores. Primary pores are normally most easily observed in dorsal views of spermathecae. Their presence defines the spermathecal head. The heads are of highly variable form: membranous to heavily sclerotized (Figs. 1-3) and variously lobed and distinct (Figs. 4, 20, 33, 38, 42) to essentially indistinguishable (except for the primary pores) from the rest of the vulval ducting (Figs. 12, 18).

The dictynoid pores occur as a single, porous plate in the bottom of a shallow, circular concavity (Figs. 2, 6, 12, 21) located on the spermathecal stalk. In some cybaeid species the porous plate is everted (Bennett 1991, Figs. 454, 457, 544). In cleared specimens the pore plate

can be seen to traverse the wall of the spermathecal stalk (Figs. 10, 15, 17, 19) and often it appears to be more or less extended into the lumen of the stalk (Figs. 14, 22, 26). The spermathecal stalk serves to connect the head with the spermathecal base. As in the head, the stalk is of variable form: distinct and bulbous (Fig. 4) to slender and indistinguishable from the rest of the spermatheca (Bennett 1991, Figs. 511, 516, 530) to at least partially incorporated into the base (Figs. 10, 14, 19, 23). The stalk is normally well sclerotized.

Pore Distribution

All taxa examined have primary pores. Of the above *Tegenaria domestica*, *Rubrius antarcticus*, the cybaeids, dictynids (except for *Dictyna coloradensis*), hahniids (except for *Neocryphoeca gertschi*), and *Argyroneta aquatica* all (apparently) have *Cybaeus*-type dictynoid pores. *Agelenopsis potteri* and *Phrurotimpus alarius* have primary pores in two distinct groups, one comprising one or a few pores and the second with many. The lycosid and the amaurobiids (exclusive of *Rubrius*) have primary, but lack dictynoid, pores.

Taxa with dictynoid pores:

CYBAEIDAE: Bennett (1991) documented primary and dictynoid pores in all known Nearctic cybaeid species except for some species of *Cybaeota* which were not specifically examined for pores. For detailed descriptions of cybaeid vulvae see Bennett (1988, 1991). A few representatives are presented here.

1. *Cybaeus* spp. (Figs. 1-6). The species of this genus generally have distinct spermathecal heads, stalks, and bases with numerous small primary pores dorsally on the heads and a single, conspicuous dictynoid pore distally on each stalk close to the junction with the spermathecal base. In some species the dictynoid pore is incorporated into the spermathecal base (Bennett 1991, Figs. 421, 430).
2. *Cybaeota shastae* (Figs. 10-11). A few primary pores are located on an inconspicuous, membranous lobe near to the atrium (Fig. 11). Each spermathecal stalk is short and simple with the dictynoid pore incorporated into the wall of the spermathecal base (Fig. 10).
3. *Cybaeozyga heterops*, in AMNH. The copulatory apparatus of *C. heterops* was not drawn during this study. Its minute epigynum and vulva correspond closely to Roth and Brame's (1972, Fig. 25) drawing of uncleared genitalia. The single transverse atrium apparently opens laterally directly into each half of the vulva. Copulatory ducts are very short. Head, stalk, and base of each spermatheca are combined into a transversely oriented, oblong bulb. Each bulb bears medially on its anterior margin a dictynoid pore and on its anterior inner lateral margin one or, at most, a very few primary pores. Each bulb is antero-posteriorly divided internally into halves with the inner half bearing the primary pore(s) and the outer half the dictynoid pore.

DICTYNIDAE:
1. *Blabomma californica* (Fig. 12). This species of *Blabomma* has a single, transverse atrium medially on the epigynum with very short copulatory ducts broadly and shallowly joined across its anterior margin. The head of each spermatheca (with a small, dorsal group of primary pores) is very close to the atrium at the beginning of and continuous with a short, well sclerotized spermathecal stalk. The stalk leads into a large, thick-walled, bulbous base with a simple lumen and bearing a large, conspicuous dictynoid pore dorsally at the junction

of stalk and base. The fertilization duct exits the base posteriorly close to the entrance of the stalk.

2. *Cicurina bryantae* (Figs. 17-18). The genus *Cicurina* shows a wide range of genitalic form (see figures in Chamberlin and Ivie 1940). The female copulatory apparatus of *C. bryantae* is representative of the simplest form and is similar to that of *Blabomma californica*. Here the atrium is a single, transverse opening posteriorly located on the epigynum (Bennett 1985, Figs. 3, 5). The copulatory ducts are relatively large, broad, anteriorly directed and weakly joined at the midline of the vulva. The lumina of the copulatory ducts gradually narrow anteriorly and the ducts lead directly into the more heavily sclerotized spermathecal heads near the anterior margin of the vulva. Primary pores are found both dorsally and ventrally on the heads. The heads are continuous with the spermathecal stalks which extend to the anterior margin of the vulva then turn posteriorly to join ventrally with the spermathecal bases at the posterior margin of the vulva. The bases are oblong, bulbous, and have simple lumina. Each base has a single, large dictynoid pore on its inner lateral margin near the entrance of the stalk. The fertilization ducts exit the bases posteriorly.

3. *Cicurina intermedia* (Fig. 15), *Cicurina* sp. (Fig. 16). These two species are representative of those *Cicurina* with more complex vulvae. The former has a single, large, transverse, oval atrium with the copulatory ducts very shallowly joined across its anterior margin. The ducts are fairly narrow and lead to the anterior vulval margin. Here the lumen of each becomes very narrow for a short distance then broadens into the spermathecal head which bears a few primary pores dorsally. The spermathecal stalks are long, convoluted, simple ducts continuous with but of slightly narrower diameter than the heads. Distally each stalk is greatly expanded and bulbous and bears a large dictynoid pore as well as the fertilization duct. Posteriorly a narrow duct leads from this bulb into a second, blind one which is probably the spermathecal base. The unidentified species considered here differs in having a much smaller atrium, a larger region of joined copulatory ducts, slightly different placement of the primary pores, and longer spermathecal stalks.

4. *Yorima angelica* (Figs. 13-14), in MCZ. Here the atria are paired, comma-like depressions found near the midline of the epigynum. The vulva in this species is relatively simple. The copulatory ducts are short, anteriorly directed, and contiguous but with separate lumina. Unfortunately primary pores were not looked for and their presence cannot be confirmed. It is predicted, however, that they are at the anterior end of the vulva where the ducting turns posteriorly. The spermathecal stalks are short and straight and enter the bulbous bases dorsomedially. A large dictynoid pore is located on each base at the junction with the stalk. The lumina of the bases are relatively complex. Fertilization ducts exit the bases posteriorly.

AMAUROBIIDAE:

1. *Rubrius antarcticus* (Fig. 21), in AMNH. In this species the paired atria are widely separated at the posterolateral margins of the epigynum (Lehtinen 1967, Fig. 160; Roth 1967, pl. 52 Fig. 12). The copulatory ducts are long. They proceed towards the midline from the atria, then to the anterior epigynal margin, then reversing direction to the posterior margin before joining the spermathecae posterolaterally dorsal to the atria. The spermathecae are unipartite and bulbous with a small group of primary pores anteriorly and a large dictynoid pore posterodorsally between the entry of the copulatory duct and the exit of the fertilization duct. The lumina of the spermathecae are undivided.

AGELENIDAE:
1. *Tegenaria domestica* (Figs. 25-30). The atrium is single and posteriorly located on the epigynum in this species (Roth 1968, Fig. 16). The copulatory ducts are broadly and shallowly joined along the anterior margin of the atrium and lead into compact, unipartite, laterally located spermathecae. The lumina of the spermathecae are compartmentalized. Primary pores are on the outer lateral margin (one large, round pore) and medially (one or a few small pores) on each spermatheca. A large, bean-shaped dictynoid pore is situated near the inner lateral margin. The two large pores are here differentiated as primary and dictynoid pores on the basis of their internal structure as seen in cleared vulvae: the dictynoid pore appears to have a complex sieve plate structure while the primary pore is simple.

ARGYRONETIDAE:
1. *Argyroneta aquatica* (Figs. 7-9), in AMNH. This is another species with a very simple, compact vulva. The atria are paired and widely separated at the lateral margins of the epigynum (Roberts 1985, Fig. 68a). Short copulatory ducts open into compact, bulbous spermathecae. One or a few primary pores are located anterodorsally close to the inner lateral margin of each spermatheca and near to the entrance of the copulatory duct and exit of the fertilization duct. A single, large, anteriorly located dictynoid pore is near the primary pores but closer to the outer lateral margin of each spermatheca. The lumina of the spermathecae appear to be compartmentalized but the very thick walls of the spermathecae make this difficult to ascertain.

HAHNIIDAE:
1. *Calymmaria montavencis* (Fig. 20), *Calymmaria* sp. (Fig. 19). Both of these species have a single small atrium located anteriorly on the epigynum (Bishop and Crosby 1926, Fig. 53) and very short copulatory ducts. In *C. montavencis* the heads of the spermathecae are short lobes projecting anteriorly from the region of the atrium and bearing primary pores apically. The stalks in this species have thick walls, narrow lumina, and lead from the atrial region to the posterior margin of the vulva. There they turn anterolaterally and enter the large, bulbous spermathecal bases. A dictynoid pore is incorporated into the dorsolateral wall of each base at its junction with the stalk. The fertilization duct exits each base adjacent to the entry of the stalk. The unidentified species is very similar except that the atrium is the anteriormost component of the copulatory apparatus and the spermathecal heads are small dorsal vulval lobes located somewhat posterior of the atrium.
2. *Dirksia cinctipes* (Figs. 23-24, 31-32). This species has paired, longitudinal atria running along the midline of the vulva (Chamberlin and Ivie 1942, Fig. 37). Short, small, and separate copulatory ducts enter the spermathecae anteriorly. Each spermatheca is simple, bulbous, and possesses an interesting arrangement of pores. The dictynoid pore is located near the outer anterolateral margin opposite the entrance of the copulatory duct. The primary pores are in two groups: a single pore on a slight prominence just posterior to the dictynoid pore and, further posteriorly, a group of pores within a small pit. The lumina of the spermathecae are undivided and the fertilization ducts are small and inconspicuous posteriorly.
3. *Neoantistea* sp. (Fig. 22). Although Opell and Beatty (1976) recently revised the Nearctic hahniids this species cannot readily be placed in any of the described ones. It has the spiracle placement characteristic of *Neoantistea* but lacks the large bulbous spermathecal component (base ?) evident in most species (see figures in Opell and Beatty). The atria here are paired, small, inconspicuous, and anteriorly located on the epigynum. The copulatory ducts are very

short, leading immediately into the spermathecae. At the anterior end of each spermatheca is a small, lateral head with primary pores posteriorly. The rest of the spermatheca is a convoluted tube of relatively constant diameter with a terminal dictynoid pore and fertilization duct.

4. *Ethobuella tuonops* (Figs. 33-34). The atria in this species are paired and open at the anterolateral corners of a common, concave "scape." The copulatory ducts are extremely short, almost nonexistent. The spermathecae are somewhat complex, each having two anteriorly directed lobes with simple lumina and a larger posterior component with a compartmentalized lumen and a short, posterior fertilization duct. A single primary pore is on the anterior tip of the smaller of the two anterior lobes. The probable presence of a dictynoid pore is indicated by a nonconformity visible dorsally on the posterior component.

5. *Cryphoeca exlineae* (Fig. 35). The paired atria of this species are anteromedially located on the epigynum. They open into broad copulatory ducts which spiral anteriorly through more than 360°. The spermathecal head is a small anterolateral lobe bearing a single, posteriorly directed primary pore. At the anterior margin of the vulva the ducting (spermathecal stalk?) of each spermatheca turns posteriorly and passes through a very narrow bottleneck bearing an apparent dictynoid pore. This region is enveloped by the distal end of the copulatory duct making it difficult to verify the presence of the dictynoid pore. The remaining ducting (spermathecal base) is broad, slightly sinuous and bears a fertilization duct posteriorly.

6. *Neocryphoeca beattyi*, *N. gertschi* (holotype specimens in AMNH). New figures of the epigyna and vulvae of these species were not prepared for this study. The atrium in *N. gertschi* is transverse, posterior on the epigynum, and more or less single (being weakly continuous across the midline of the epigynum). The atria are similar in *N. beattyi* but are paired. Both species have sinuous, well sclerotized copulatory ducts proceeding anteriorly (Roth 1970, Figs. 2, 3). Close to the junction of each copulatory duct with a less well sclerotized spermatheca is a single anteriorly directed primary pore. These are visible ventrally and medially in the vulvae of *N. beattyi* and on the outer anterolateral vulval margins in *N. gertschi*. The spermathecae in the latter are large, relatively simple bulbs in which dictynoid pores have not been observed. The more complex and convoluted spermathecae of *N. beattyi* have a dictynoid pore hidden on the dorsal surface of an anteroventral blind lobe.

Taxa without dictynoid pores:

AGELENIDAE:
1. *Agelenopsis potteri* (Figs. 36-38). The vulvae of the species of *Agelenopsis* are complex. Their structure was described in detail by Gering (1953—various species) and Petrunkevitch (1925—*A. naevia*), but neither author noted the presence of primary pores distally on the "blind duct of the diverticle" (Figs. 37-38). Their "diverticle" is probably homologous to the spermathecal head. Both noted a primary pore bearing "blind tube" ventrally on the most heavily sclerotized component of the vulva. In *A. potteri* a similar "blind tube" is lacking but there are numerous primary pores ventrally on the heavily sclerotized component close to the exit of the fertilization duct (Fig. 36).

AMAUROBIIDAE:
1. "*Coelotes*" sp. (Fig. 41), in CNC; *Coras juvenilis* (Fig. 39); *Wadotes calcaratus* (Fig. 40). These three representatives of the coelotines all possess primary pores on more (Figs. 39-40)

or less (Fig. 41) well developed, lobe-like, spermathecal heads. The spermathecal ducting in *Wadotes* and especially in *Coras* becomes increasingly sclerotized and complex distally. The compact and very heavily sclerotized nature of the entire vulva in the "*Coelotes*" species examined precluded the complete determination of the complex duct trajectories.

2. *Callioplus macarius* (Fig. 44). In this species the vulva is very simple, compact, and heavily sclerotized. A small number of primary pores are located medially on the outer lateral margin of each spermatheca.

DICTYNIDAE:

1. *Dictyna coloradensis*. Unfortunately no good illustrations of the vulva of this species appear to exist and none was made during its examination for this study. Chamberlin and Gertsch (1958, pl. 26 Fig. 4) figured only the epigynum with its paired atria. Both they (Chamberlin and Gertsch 1958, various figs.) and Roberts (1985, Fig. 14) did publish figures of the vulvae of some other species of *Dictyna* but either the species figured lack or (more likely) these authors missed observing spermathecal heads as possessed by *D. coloradensis*. In this species primary pores are located distally on a relatively long, loosely coiled, membranous tube attached to each copulatory duct near the atria. This structure is easily overlooked and is presumed to exist in some form in other species of *Dictyna*.

LYCOSIDAE:

1. *Hogna helluo* (Figs. 42-43). In common with many other lycosines (see figures in Dondale and Redner 1990) this species has an anteriorly directed lobe distally on each spermatheca. In this species (and probably all the other lycosines with this feature) the lobe bears primary pores and is here considered to be the spermathecal head.

LIOCRANIDAE:

1. *Phrurotimpus borealis*, in CNC. This species is similar to *Agelenopsis potteri* in that it possesses two sets of primary pores. Here, however, they are located together on the most posterior and heavily sclerotized component (spermatheca?) of the vulva (see Dondale and Redner 1982, Fig. 246). The outer anterolateral margin of each spermatheca bears a single primary pore on the apex of a small nipple. The dorsal surface of each spermatheca is liberally scattered with other primary pores.

Discussion

This study provides further support for the hypothesis of primitive presence of primary pores in the vulva of all spiders. All spiders examined specifically for these structures have them. Dictynoid pores are present in all the dictynoid taxa examined so far except for *Neocryphoeca gertschi* and *Dictyna*. Some putative dictynoid groups such as the desids and anyphaenids have not been examined for this character.

Among spiders usually considered to be non-dictynoid, dictynoid pores have been found in *Tegenaria* (Agelenidae) (Figs. 25-30) and *Rubrius* (Amaurobiidae) (Fig. 21). Perhaps these two genera would be better placed in Dictynoidea. *Tegenaria* has traditionally been considered an agelenid because of its possession of plumose hairs, elongated posterior spinnerets, and a single row of tarsal trichobothria increasing in length distally. The first and third characters are plesiomorphic (see discussions in Bennett 1991:35-36 and especially Coddington 1990b:7; Fig. 3,

characters 8 and 9; and Table 1, character 49) and the second is too variable and poorly defined to be diagnostic. *Rubrius* was transferred from the Agelenidae (Cybaeinae) to the Amaurobiidae (Macrobuninae) by Lehtinen (1967) (i.e., from Dictynoidea to Amaurobioidea) apparently on the basis of overall similarity not apomorphy. However, at this point neither *Tegenaria* nor *Rubrius* can be placed in a specific dictynoid family (as opposed to Dictynoidea *incertae sedis*). Until other character systems such as trichobothria and spinneret spigots are analyzed for these taxa it is preferable to consider their possession of dictynoid pores as homoplasy and leave them in their current placements with the knowledge that their sister taxa may be dictynoid and not amaurobioid.

Coddington (1990a) postulated the following cladistic relationship: (Amaurobioidea (Dictynoidea, Orbiculariae)). No Orbiculariae were specifically examined for dictynoid pores but published SEM and compound microscope photographs of the vulvae of various orbicularian taxa (e.g. *Latrodectus*, Foelix 1982; Anapidae, Platnick and Forster 1989) show no indication of any structure comparable to a dictynoid pore. This, coupled with discussions with current students of orbicularian systematics, indicates that dictynoid pores do not exist in Orbiculariae.

Coddington (1989) proposed that possession of a highly branched tracheal system is an apomorphy of Dictynoidea *sensu* Forster (1970). I suggest that the dictynoid pore is a second apomorphy of Dictynoidea or at least those dictynoid families in which this pore has been observed.

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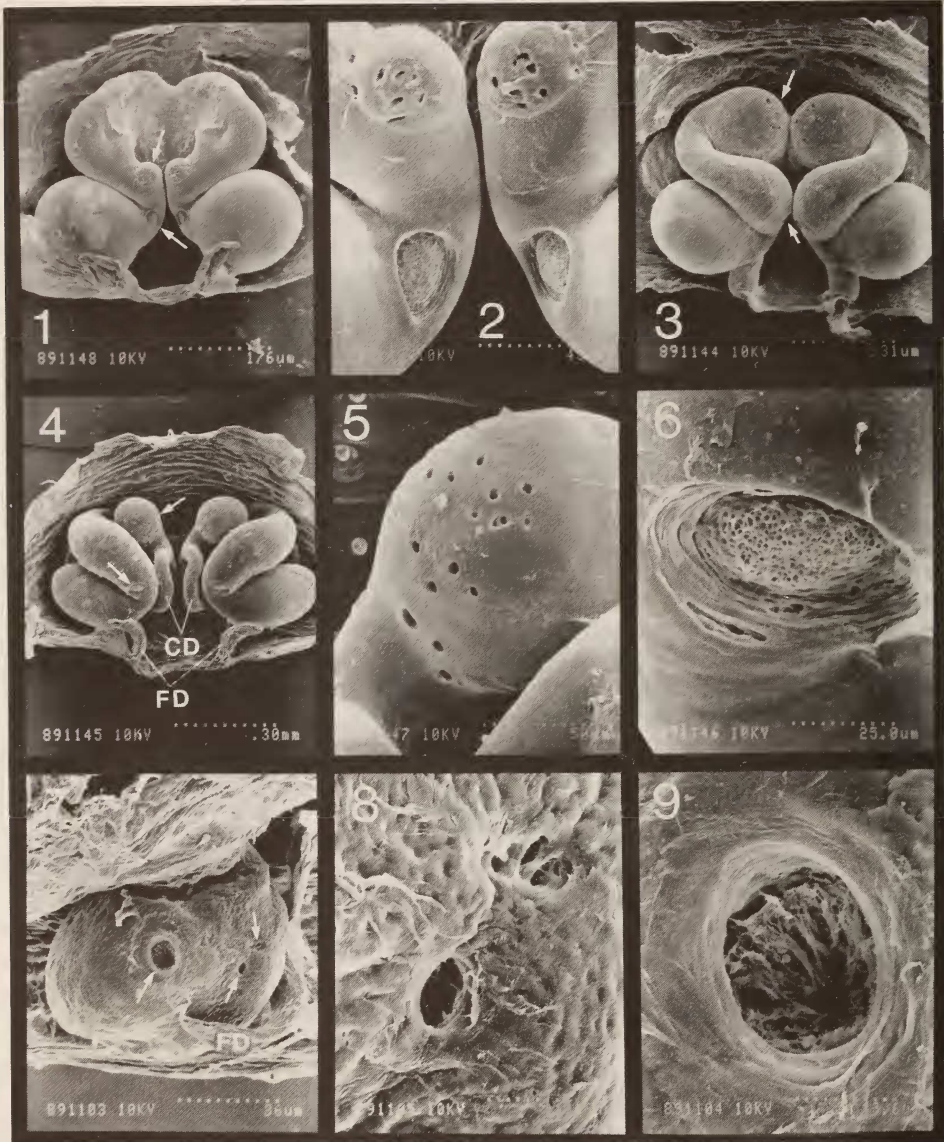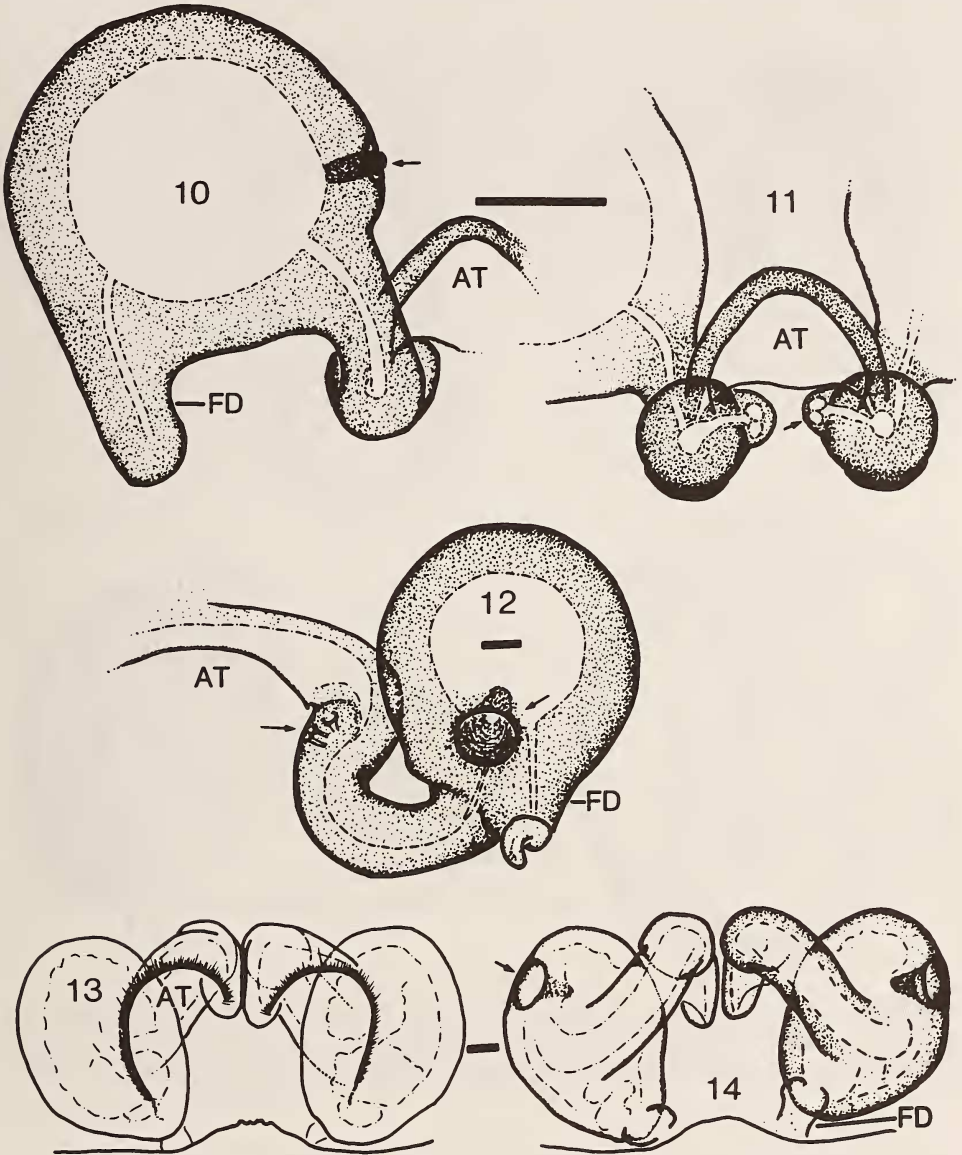
FIGURES 1-9. Vulvae and pores: 1, *Cybaeus grizzlyi*, dorsal; 2, detail of Fig. 1; 3, *Cs. morosus*, dorsal; 4, *Cs. signifer*, dorsal; 5, detail (primary pores) of Fig. 4; 6, detail (dictynoid pore) of Fig. 4; 7, *Argyroneta aquatica*, one-half of vulva, anterodorsal; 8, detail (primary pores) of Fig. 7; 9, detail (dictynoid pore) of Fig. 7. Arrows indicate pores. CD—copulatory ducts, FD—fertilization ducts.

FIGURES 10-14. Vulvae and pores: 10, *Cybaeota shastae*, Victoria BC, dorsal; 11, same, ventral; 12, *Blabomma californica*, Victoria BC, dorsal; 13, *Yorima angelica*, Baja California, ventral; 14, same, dorsal. Arrows indicate primary and dictynoid pores. Scale bars = 0.025 mm. AT—atrium.
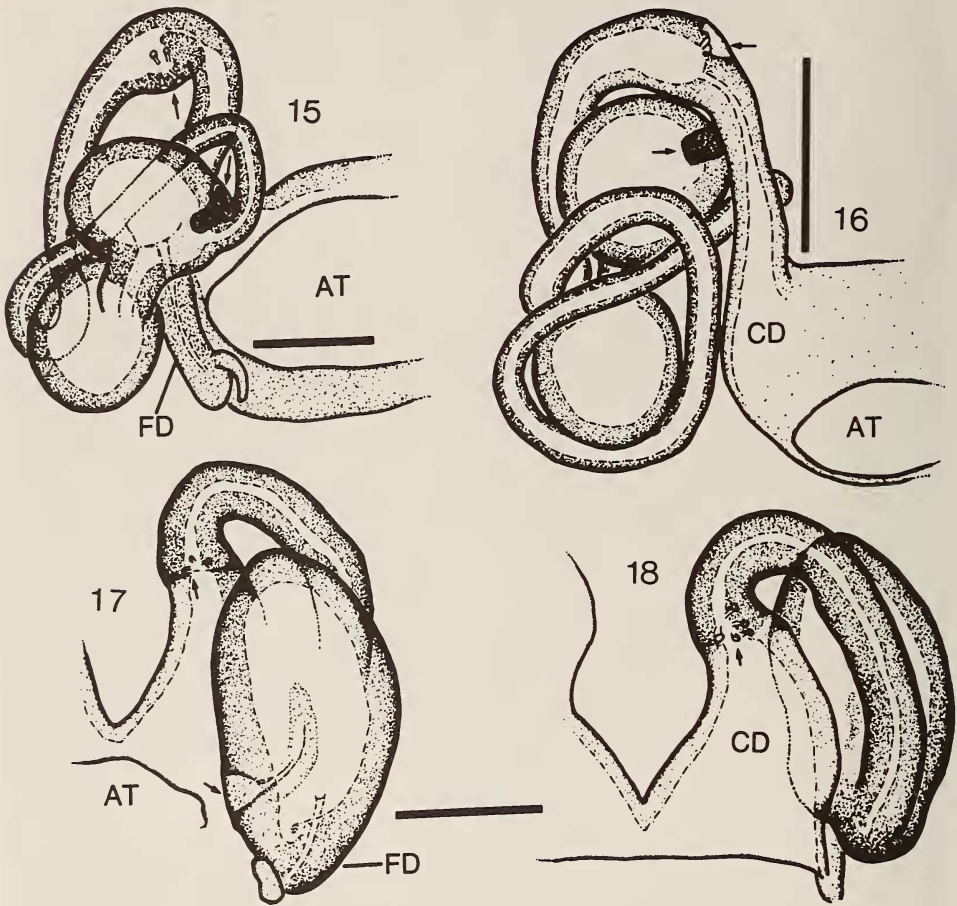
FIGURES 15-18. *Cicurina* spp., vulvae and pores: 15, *C. intermedia*, Wallowa Co. OR, dorsal; 16, *C.* nr. *cavealis*, St. Lawrence Is. Nat. Pk. ON, ventral; 17, *C. bryantae*, Graham Co. NC, dorsal; 18, same, ventral. Arrows indicate primary and dictynoid pores. Scale bars = 0.10 mm.
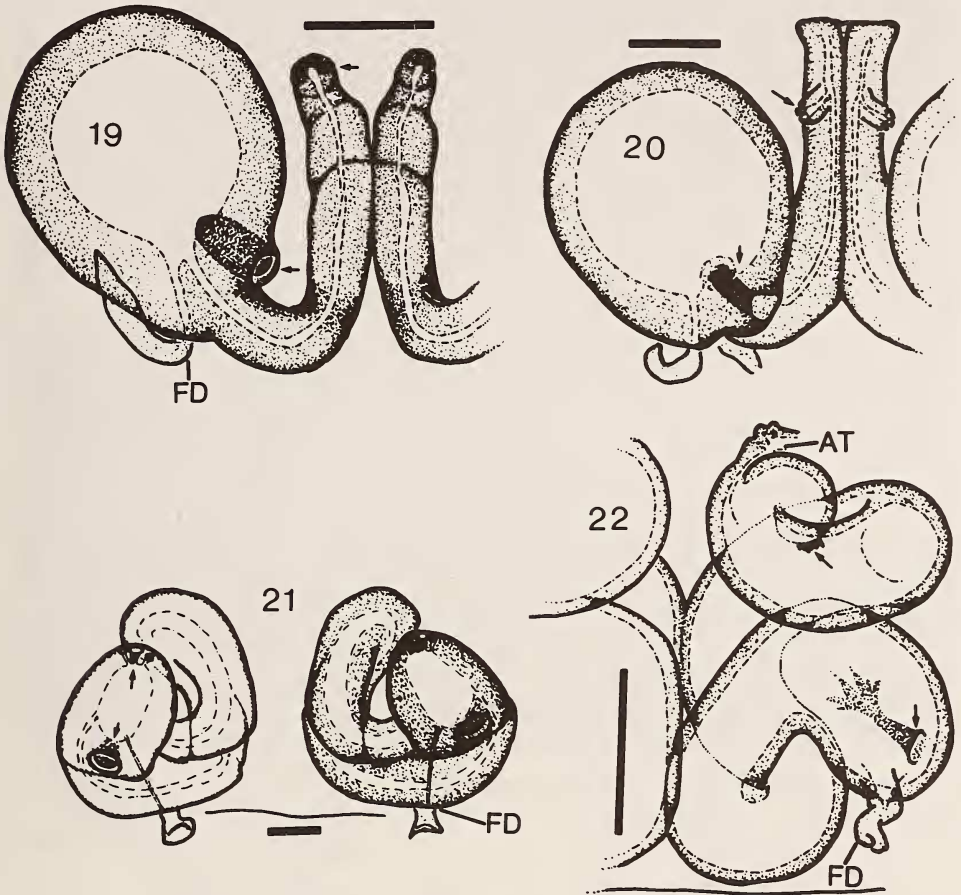
FIGURES 19-22. Vulvae and pores, dorsal: 19, *Calymmaria* sp., Skamania Co. WA; 20, *C. montavencis*, Great Smoky Mtn. Nat. Pk. NC; 21, *Rubrius antarcticus*, Isla Guarello, Magallanes, Chile; 22, *Neoantistea* sp., Great Smoky Mtn. Nat. Pk. NC. Arrows indicate primary and dictynoid pores. Scale bars = 0.10 mm.
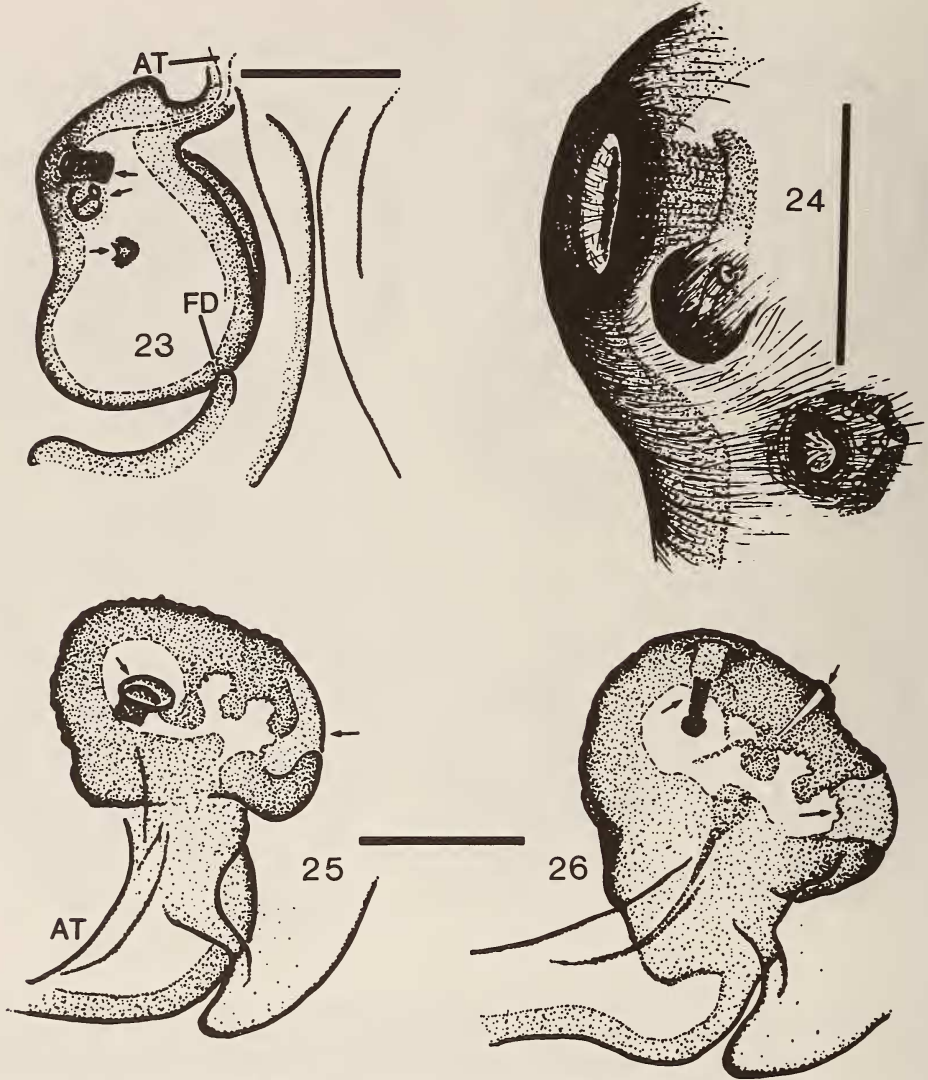
FIGURES 23-26. Vulvae and pores: 23, *Dirksia cinctipes*, North Vancouver BC, dorsal; 24, detail of Fig. 23; 25, *Tegenaria domestica*, Victoria BC, ventral; 26, same, Saanich BC, ventral. Arrows indicate primary and dictynoid pores. Scale bars = 0.05 mm.
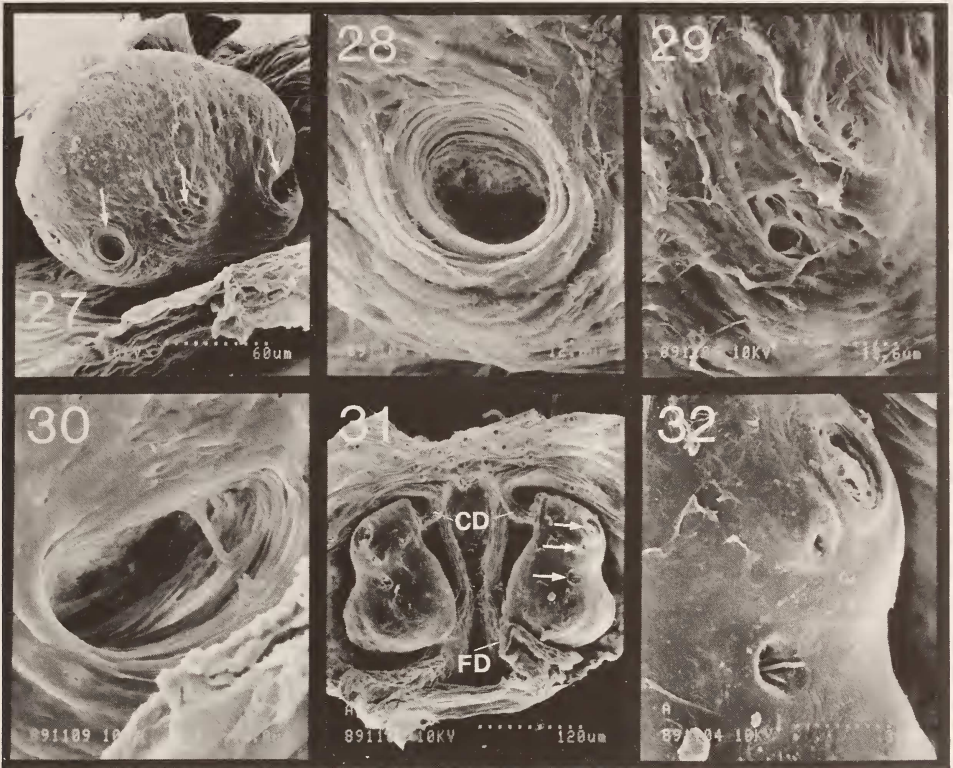
FIGURES 27-32. Vulvae and pores: 27, *Tegenaria domestica*, one-half of vulva, anterodorsal; 28-30, details of Fig. 27; 31, *Dirksia cinctipes*, dorsal; 32, detail of Fig. 31. Arrows indicate pores.
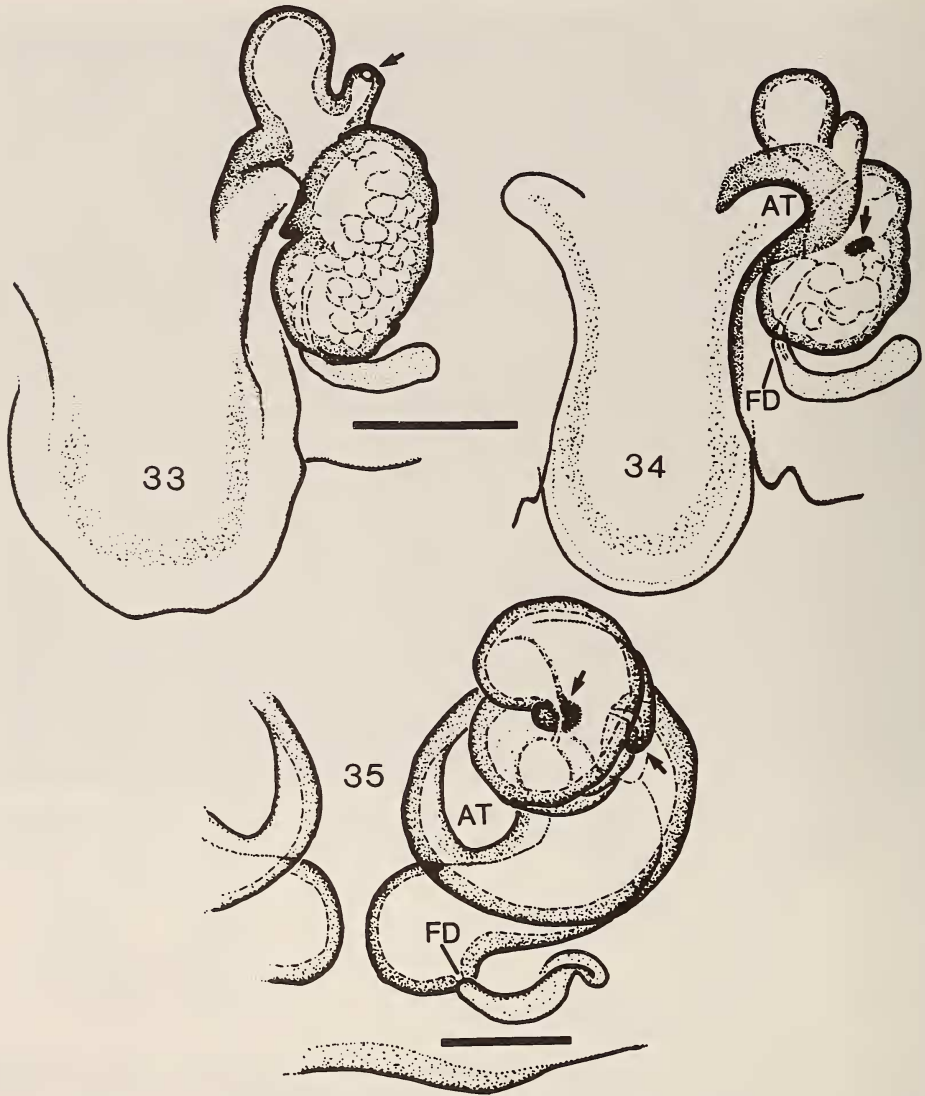
FIGURES 33-35. Vulvae and pores: 33, *Ethobuella tuonops*, Victoria BC, dorsal; 34, same, ventral; 35, *Cryphoeca exlineae*, Glacier Nat. Pk. BC, dorsal. Arrows indicate primary and dictynoid pores. Scale bars = 0.10 mm.
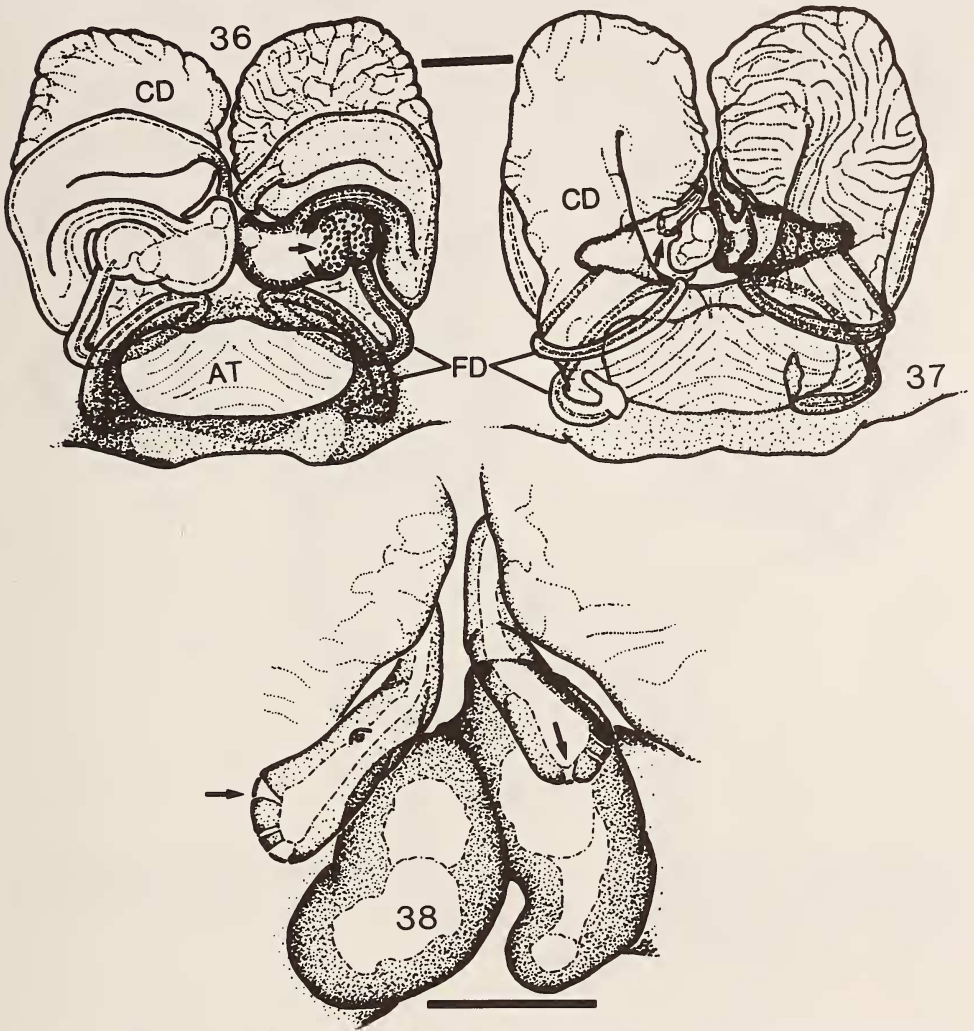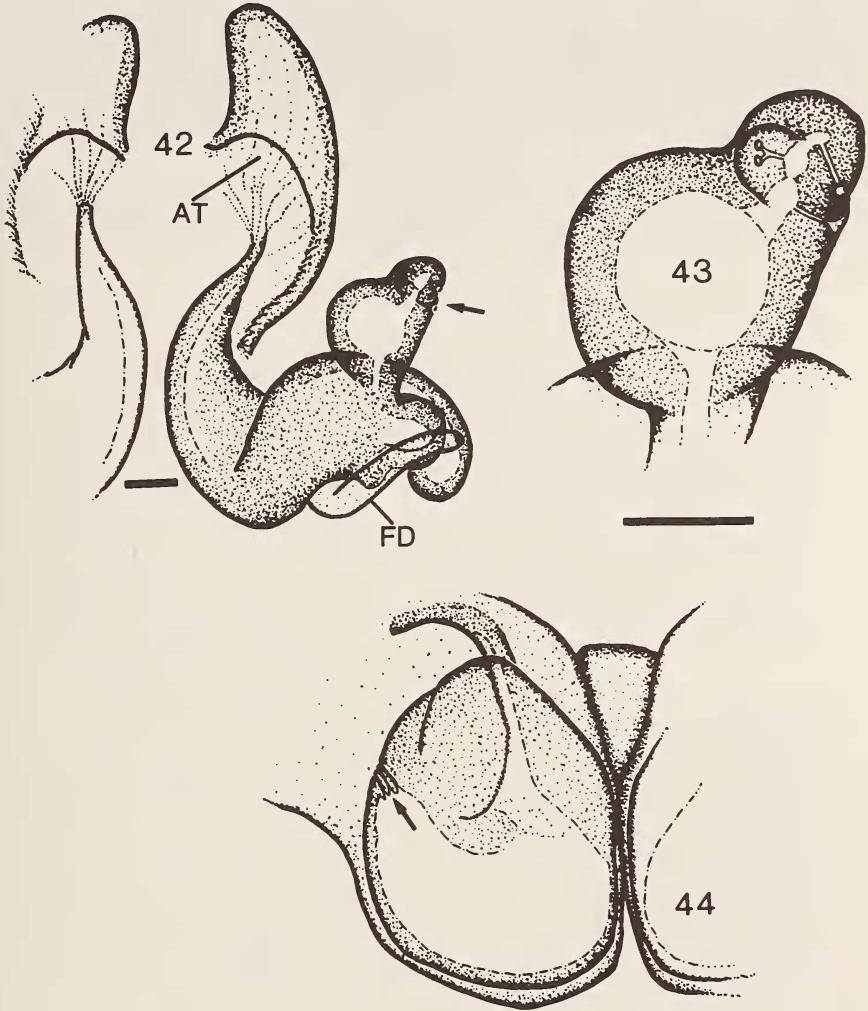
FIGURES 36-38. Vulva and pores, *Agelenopsis potteri*, Guelph ON: 36, ventral; 37, dorsal; 38, detail of Fig. 37. Arrows indicate pores. Scale bars = 0.10 mm.
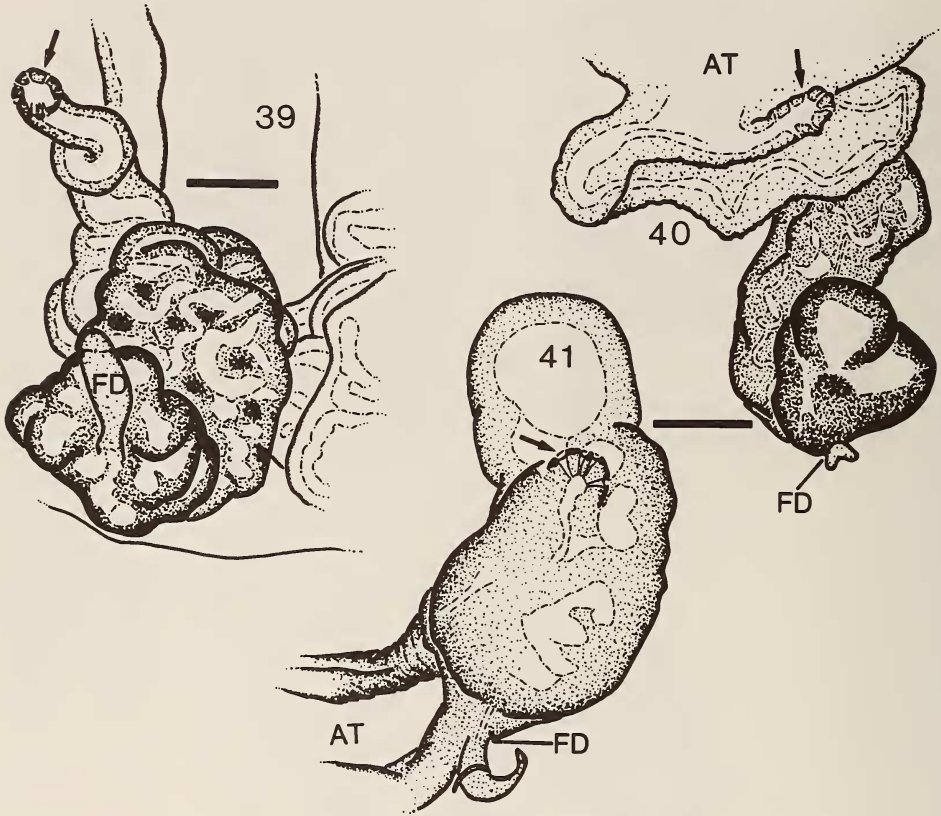
FIGURES 39-41. Vulvae and pores, Coelotinae: 39, *Coras juvenilis*, Furnessville IN, dorsal; 40, *Wadotes calcaratus*, Halton Co. ON, anterodorsal; 41, "*Coelotes*" sp., near Ghopte Nepal, dorsal. Arrows indicate primary pores. Scale bars = 0.10 mm.

FIGURES 42-44. Vulvae and pores, dorsal: 42, *Hogna helluo*, Port Carling ON; 43, detail of Fig. 42; 44, *Callioplus macarius*, Lane Co. OR. Arrows indicate primary pores. Scale bars = 0.10 mm.